THE ROYAL SOCIETY

Hybridizing Old and New World camelids: *Camelus dromedarius* × *Lama guanicoe*

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Thirty female dromedary camels were inseminated on a total of 50 occasions with 2–4 ml of fresh guanaco semen diluted with an equal volume of commercially available camel semen extender. Similarly, nine female guanacos were inseminated on 34 occasions with 4–6 ml of fresh, diluted camel semen. Only two of the dromedary females conceived; one aborted a female foetus on day 260 of gestation and the other gave birth to a stillborn female calf on day 365. Six conceptions occurred in the female guanacos. Two of these conceptuses, diagnosed by ultrasound, were resorbed between days 25 and 40 of gestation, one female foetus was aborted on day 291, another female foetus was aborted on day 302, and one female calf was stillborn on day 365 of gestation. The sixth foetus, a male, was born prematurely but alive after a 328-day gestation. It had a phenotypic appearance intermediate between that of a camel and a guanaco and its hybrid parentage was confirmed by the DNA fingerprinting of eight llama microsatellites. To our knowledge, this is the first viable hybrid ever to be produced between Old World and New World camelids, which have been reproductively isolated from one another for at least 11 million years. The preponderance of female hybrids is in accordance with Haldane's law. Histological examination of their ovaries revealed a failure of meiosis, with only an occasional abnormal oocyte surrounded by follicle cells. Although the diploid chromosone number of camels and guanacos is the same ($2n = 74$), sufficient genetic change has taken place to make the pairing of homologous chromosomes no longer possible.

Keywords: camel; guanaco; hybrid

1. INTRODUCTION

The family Camelidae is of great antiquity. Palaeontological evidence suggests they split off from the other cloven-hoofed mammals in the Eocene *ca.* 40–45 million years (Myr) ago (Romer 1966; Simpson 1980), and split again into the genera *Camelus* and *Lama* in North America relatively soon after, *ca.* 30 Myr ago (Webb 1974; Harrison 1979). However, more recent molecular studies of mitochondrial DNA (mtDNA) mutation rates suggest that the split may have occurred *ca.* 11 Myr ago (Stanley *et al.* 1994). Today, there remains two species of large, Old World camels indigenous to Asia and Africa, namely, the two-humped Bactrian (*Camelus bactrianus*) and the one-humped dromedary (*Camelus dromedarius*), and four species of smaller New World camels in South America, the domesticated llama (*Lama glama*), its probable wild antecedent the guanaco (*Lama guanicoe*), the domesticated alpaca (*Lama pacos*) and its possible wild ancestor the vicuña (*Lama vicugna*). During one of the early ice ages, the cameloids crossed the land bridge created between North America and Asia in the region of the Bering Straits and then radiated through Asia into Eastern Europe and the Middle East. They were unknown to the ancient Egyptians (Zeuner 1963), and may have been introduced into North Africa by man. The lamoids migrated southwards and crossed the land bridge into South America. All Camelidae had become extinct in North America before historic times.

Today, the New and Old World camelids show some remarkable anatomical and physiological similarities, and some equally striking contrasts as a result of their adaptation to different environmental extremes. For example, they all share the same diploid chromosome number ($2n = 74$; Hsu & Benirschke 1969), they are all induced ovulators (San-Martin *et al.* 1968; Musa & Abusineima 1978; El Wishy 1987) and they all have a bicornuate uterus in which the left horn is considerably larger than the right and always acts as the site of implantation—although ovulation occurs equally frequently from the left and right ovaries (Arthur *et al.* 1985; El Wishy 1988). They also share the same diffuse, non-invasive epitheleochorial placenta (Van Lennep 1963; Steven *et al.* 1980; Skidmore *et al.* 1996*a*). They differ in that the New World camelids are small, cloven-hoofed, and have a dense, fine-wool coat that enables them to survive in the extremely low temperatures of the snowy deserts of the high Andes, whereas the Old World camelids are much larger, have a single broad footpad and a less dense hairy coat, and are adapted to the extreme diurnal temperature variations

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and scarce food supplies in the mountainous deserts of Mongolia and the low-lying deserts of Arabia. Both the Old World camelids will hybridize with one another to produce fertile offspring, and all the New World species will similarly hybridize with each other and produce fertile young (Gray 1972). However, to our knowledge there are no published accounts of induced hybridization between Old and New World camelids, which could not occur naturally due to geographical separation and great disparity in body size. The object of the present study was to attempt to hybridize dromedaries with guanacos, using artificial insemination.

2. MATERIALS AND METHODS

Thirty adult female dromedary camels aged 6–14 years and estimated to weigh between 380 kg and 450 kg, and two adult male dromedaries aged five and eight years and estimated to weigh 550–600 kg that had been trained to ejaculate into a modified bull artificial vagina (AV), were maintained as part of the experimental herd at the Camel Reproduction Centre in Dubai, UAE. Nine females (estimated age, 3–7 years; estimated weights, 75–80 kg) and one young male (estimated age, 3–4 years; estimated weight, 85 kg) guanacos were captured from a nearby wildlife park, translocated to pens at the Camel Reproduction Centre and partly tamed.

During the camel breeding season in the Arabian Gulf region (November–April) of 1995–1996 and 1996–1997, the ovarian follicular wave patterns of the dromedaries were monitored by serial trans-rectal ultrasound examinations, as described by Skidmore *et al.* (1995). When a dominant follicle reached a diameter of 1.3–1.6 cm the camel was given an intravenous injection of 20 μg of the GnRH analogue, buserelin (Receptal; Hoechst Animal Health, Bedfordshire, UK). The camel was then inseminated with the whole ejaculate from a male guanaco (2–4 ml of semen; $15–40 \times 10^7$ spermatozoa; 50–70% motility) collected with the AV and diluted with an equal volume of a commercial semen extender designed for camel semen (Green Buffer; IMV Ltd, L 'Aigle, France) containing 10% v/v egg yolk. This was deposited in the body of the uterus using a plastic bovine insemination catheter guided manually through the cervix by the operator's sterile gloved hand in the vagina. These inseminations were given either once, 24 h after treatment with GnRH ($n = 45$), or twice, at the time of GnRH therapy and again 24 h later ($n = 5$).

The female guanacos were also monitored by trans-rectal ultrasonography and when the dominant follicle attained a diameter of 0.8–0.9 cm, each guanaco was given an intramuscular (IM) injection of 10 μg buserelin and inseminated either once 24 h later ($n = 22$) or twice 24 h apart ($n = 11$) with a 4–6 ml aliquot of camel semen diluted 1:1 with Green Buffer containing 10% v/v egg yolk. The inseminate was prepared from a camel ejaculate (3–8 ml; $50–150 \times 10^7$ spermatozoa; 60–80% motility) and it was also deposited in the uterine body by means of a manually guided insemination catheter passed through the cervix.

Ovulation in the camels and guanacos was diagnosed by ultrasound examination of the ovaries 48 h after the GnRH injection (Skidmore *et al.* 1995) and confirmed subsequently by measuring a rise in progesterone concentrations in peripheral serum samples recovered daily from each animal from the time of the GnRH treatment. A chemiluminescent progesterone assay developed for human serum (Amerlite; Kodak Diagnostics Ltd, Buckinghamshire, UK) and validated for camel serum by Skidmore *et al.* (1996*b*) was used. Pregnancy was suspected when serum progesterone concentrations remained elevated beyond 12 d after insemination, and was subsequently confirmed by ultrasound examination of the uterus. A discrete accumulation of conceptus fluid in the lumen of the left uterine horn was first observed between days 18 and 20, an echogenic embryo suspended within the fluid could be distinguished between days 20 and 23, and a foetal heartbeat was identifiable between days 25 and 27 (Skidmore *et al.* 1992).

In two of the inseminated camels it was suspected that luteal function was impaired, as judged, using ultrasonography, by the small size of the corpus luteum and low serum progesterone concentrations. These animals were, therefore, given daily IM injections of 6 ml of a 25 mg ml^{-1} suspension of progesterone in peanut oil (Intervet Laboratories, Cambridge, UK) from the sixth day after insemination until one of them was confirmed as non-pregnant by ultrasound examination on days 22 and 25 and the other aborted a dead and partly autolysed foetus on day 260 of gestation.

3. RESULTS

Thirty dromedary females were inseminated on 50 occasions with diluted guanaco semen 24 h after an injection of GnRH analogue was given to induce ovulation, but only two conceived (table 1). One camel aborted a dead and partly autolysed female foetus (GC2) on day 260 of gestation while still receiving progesterone therapy. The other calved unattended and spontaneously on day 365 of gestation but the female calf was stillborn (GC1). Post-mortem examination showed that the calf had developed normally but its lungs had not been aerated.

Six conceptions occurred in the nine female guanacos that were inseminated with diluted camel semen after a GnRH injection to induce ovulation on 34 occasions (table 1). One conceptus failed to develop an embryo and the vesicle shrank and disappeared ultrasonographically between 22 and 30 days after insemination (CG3). In a second guanaco, the foetal heartbeat ceased between the two serial ultrasound examinations performed 30 and 39 days after insemination, and the remaining conceptus fluid and membranes shrank and disappeared altogether over the following 20 days (CG4). One female foetus was aborted on day 291 (CG1), another female foetus was aborted on day 302 (CG6) and one female foetus was stillborn on day 365 of gestation (CG2). The sixth guanaco calved spontaneously and unaided on day 328 of gestation and produced a live male calf, Rama (CG5), that was somewhat premature and weighed only 5.5 kg. This was less than the weight of a newborn guanaco at term (8–10 kg) and appreciably less than the weight of a newborn camel calf (± 30 kg).

(a) *Rearing the calf*

The hybrid calf showed no tooth eruption at birth, an indication of its prematurity, and since its mother had no mammary development and showed no maternal behaviour, it was hand-reared on fresh camel milk obtained daily from a dromedary that had calved 24 h earlier. Initially, each feed of 30–50 ml of camel milk was offered at regular intervals, every 1.5 h throughout the day and night. After 48 h, the feeding interval was extended to 2 h

Table 1. *Hybrid pregnancies*

(C represents camel; G represents guanaco.)

hybrid number	sire	dam	date of delivery	foetal weight (kg)	sex	duration of gestation (days)
	camel	guanaco				
CG1	Musehan	3	3/11/96	2.5	female	291 (aborted)
CG2	Musehan	3	4/1/98	9.0	female	365 (stillborn)
CG3	Young One or Musehan	1	—	—	—	30 (resorbed)
CG4	Young One or Musehan	4	—	—	—	40 (resorbed)
CG5	Musehan or Young One	1	14/1/98	5.5	male	328 (born live)
CG6	Musehan	6	3/11/98	3.7	female	302 (aborted)
	guanaco	camel				
GC1	Whalid	660	18/2/97	30.0	female	365 (stillborn)
GC2	Whalid	1610	3/2/98	1.0	female	260 (aborted)

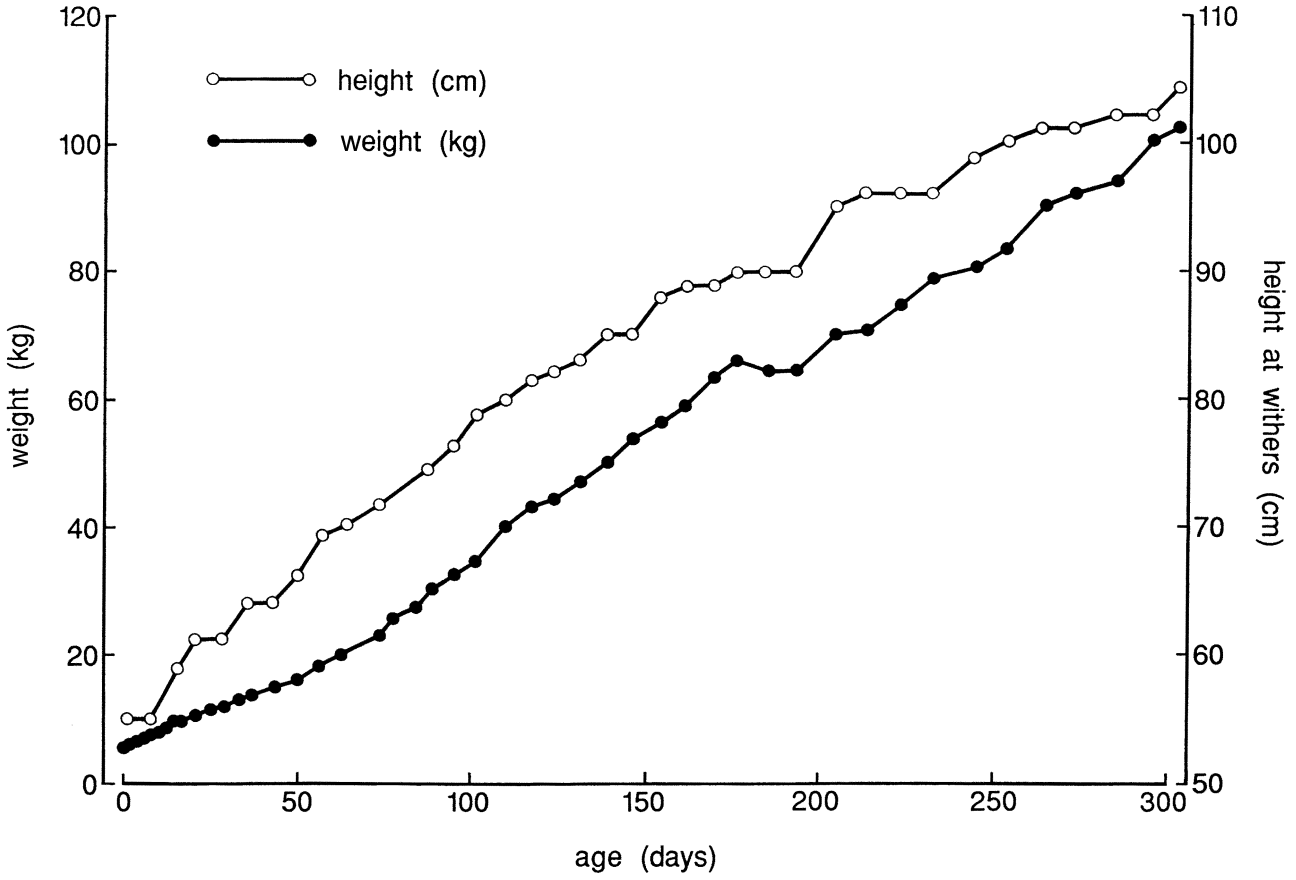

Figure 1. Growth curve for the male dromedary × guanaco calf, Rama, during the first nine months. Open circles, height in centimetres; closed circles, weight in kilograms.

and the daily intake increased to 1200 ml. This pattern was continued for the first month but, during the second and third months, the feeding interval was increased gradually to 4 h. The volume of milk consumed per feed increased from 300 ml at the end of the first month to 700 ml by the end of the fourth month, by which time the feeding interval had extended to 8 h. A compounded 'calf starter' feed and hay were offered to the calf from 30 days of age and its daily intake of these solids had increased to around 500 g by the fourth month. Initially, the calf gained weight at a rate of 0.2 kg per day over the first seven days but thereafter the gain increased to approximately 2.5 kg per week (figure 1).

At nine months of age the hybrid calf was in good health. He exhibited the woolly fibre coat and the nose and nostrils of the New World camelids, but his ears and tail were midway in length between those of camels and guanacos (figure 2*c*). Similarly, his feet were an intermediate of the single two-toed conjoined footpad of camels and the cloven hooves of guanacos (figures 2*d–f*). However, unlike guanacos, he showed no skin glands on the lateral or medial aspects of the tarsus and there was no sign of the hump that would be present on a camel calf of the same age. He had two small testicles, measuring 4 cm × 2 cm and palpable in the scrotum *ca.* 4 cm below the anus.

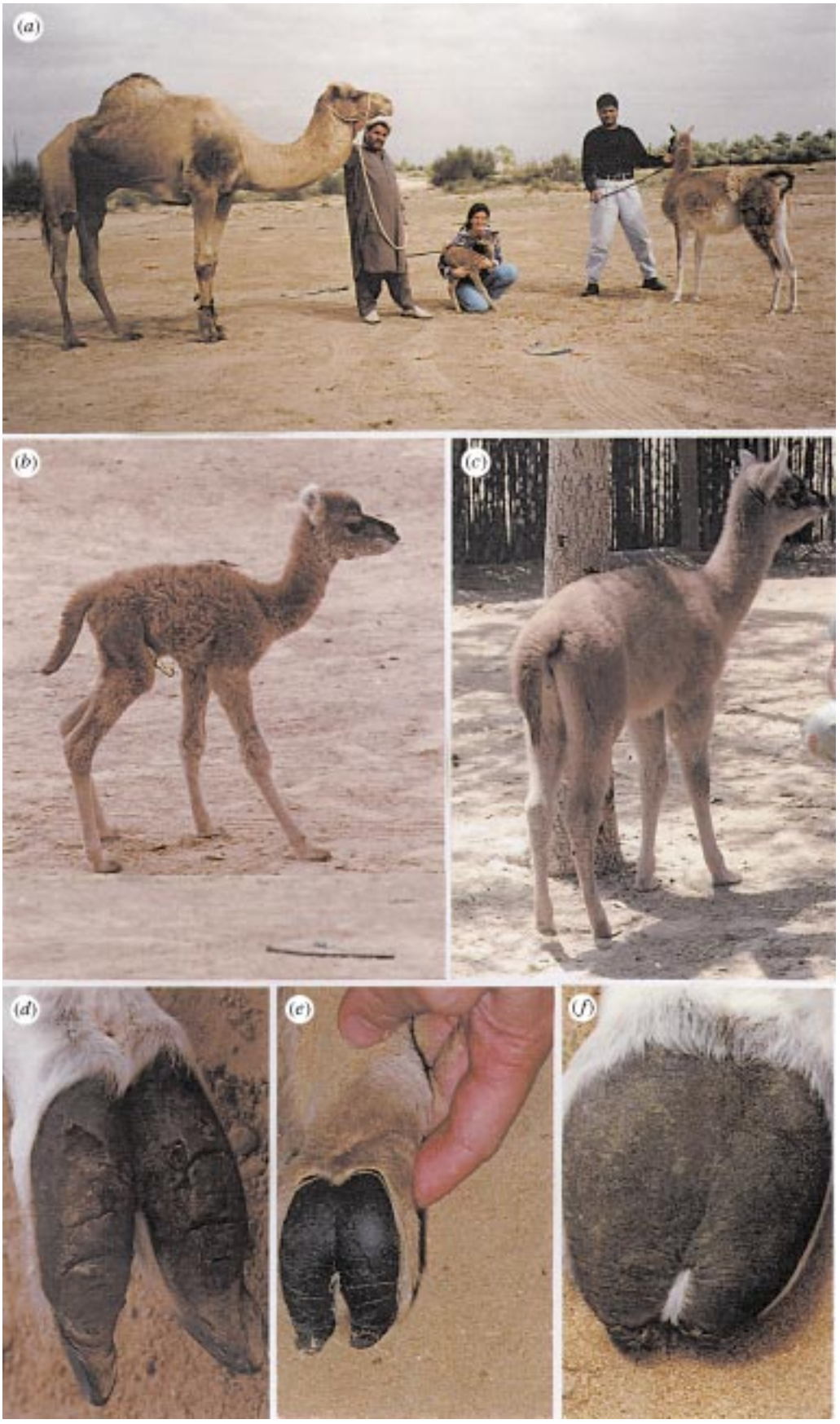

Figure 2. (*a*) The dromedary sire, Musehan, and the guanaco dam (no. 1) with their two-day old hybrid calf. (*b*, *c*) The hybrid calf, Rama, at two days and two months of age, respectively. (*d–f*) Comparison of the front footpads of (*d*) an adult female guanaco, (*e*) the dromedary × guanaco hybrid, and (*f*) a newborn dromedary camel calf.

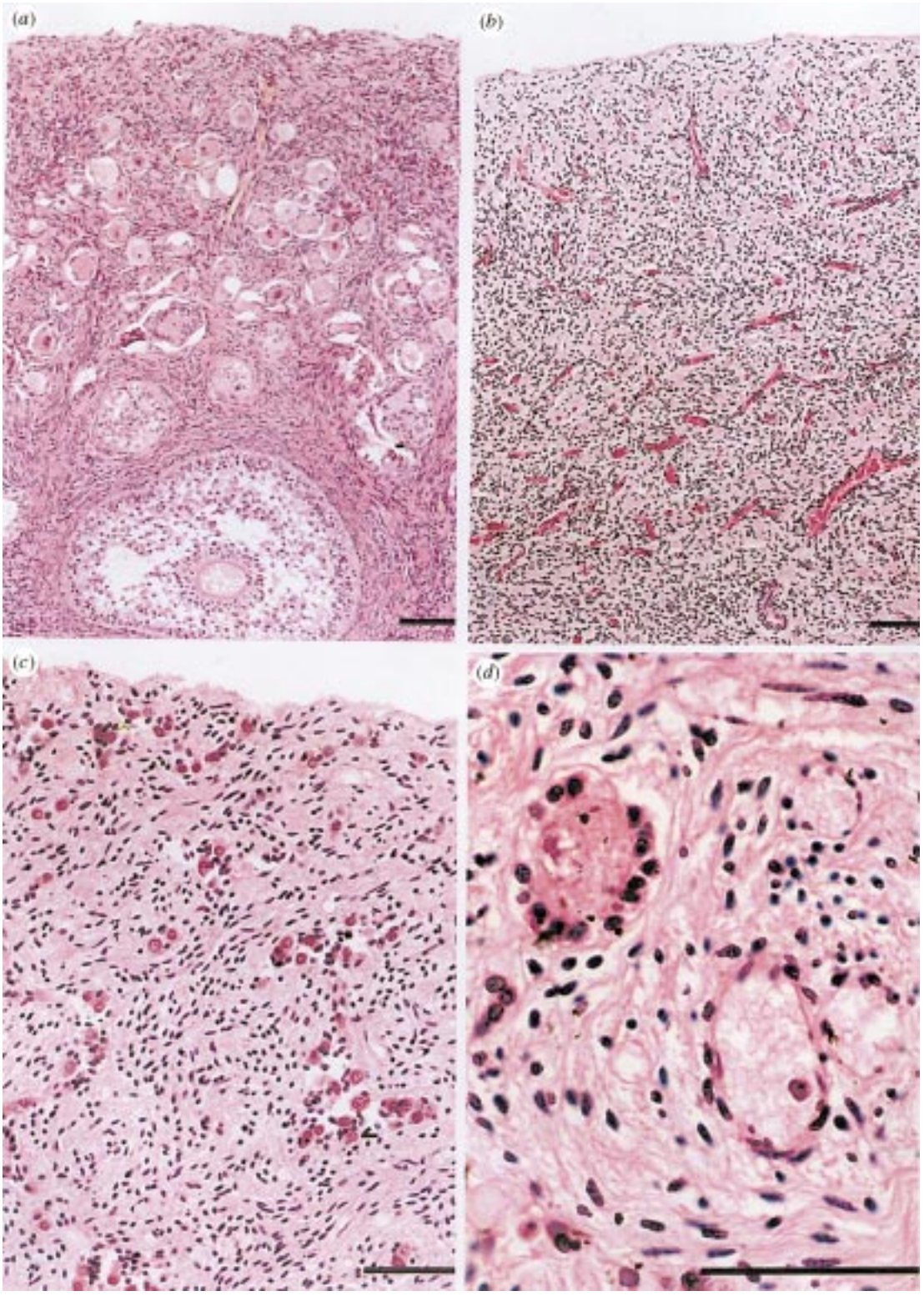

Figure 3. Histological sections of the ovaries recovered from (*a*) a full-term guanaco calf and (*b–d*) three guanaco × dromedary hybrid foetuses (see table 1). (*a*) The guanaco × guanaco calf stillborn at full term. The cortex is packed with 'normal'-looking oocytes contained within primary, secondary or tertiary follicles. (*b*) Hybrid calf CG2, showing a compact, fibrous cortex containing many eosinophylic cords which may represent dead or dying oogonia in Pflüger's cords, unable to enter meiosis. No oocytes or follicles are visible. (*c*) A high-power section of the cortical region of the ovary from hybrid GC1 showing heavily eosinophylic oogonia arranged in clumps or cords, but no oocytes or follicle cells. (*d*) A high-power section of the ovary from hybrid CG1 showing one unhealthy looking oocyte surrounded by degenerating follicle cells and an adjacent, even more degenerative, oocyte with a pycnotic nucleus and barely recognizable follicle cells. Scale bars, 100 μm.

Table 2. *Genotyping results for the eight llama microsatellites tested on the camel × guanaco hybrid and its parents*

	YWLL08	YWLL19	YWLL29	YWLL36	YWLL40	YWLL43	YWLL44	YWLL59
guanaco (no. 1)	135/143	243/243	215/217	153/155	186/186	133/133	83/112	107/111
hybrid (CG5)	135/158	243/243	205/215	133/155	172/186	133/133	83/103	107/107
Musehan	158/158	243/243	205/205	131/133	172/172	133/133	103/107	107/109
Young One	128/130	243/243	205/205	131/133	172/172	133/133	107/107	107/109

Behaviourally, Rama clearly showed features of his hybrid genotype. His vocalization was an unusual highly pitched 'croak' uttered on expiration, which has discernible elements of both parental species. He urinated backwards in a series of spurts like both guanacos and camels, but defecated while moving which is similar to camels but not guanacos, which tend to defecate in one place. He chewed cud by alternating from one side to the other in a manner similar to guanacos. He developed aggressive behaviour towards adult female guanacos, which included laying his ears back, rearing onto his hind legs, striking out with his front feet and attempting to spit; none of these movements are exhibited by young camels.

(b) *Post-mortem findings*

The ovaries of hybrid foetus GC2 were too decomposed to permit histological examination. Ovaries were recovered from the hybrid foetus, CG1, aborted on day 291 of gestation; the two hybrid calves, CG2 and GC1, stillborn on day 365; from a newborn full-term guanaco calf; and from a dromedary foetus aborted at 12 months of gestation. Pieces of ovarian tissue were fixed in 10% phosphate-buffered formaldehyde solution, embedded in paraffin wax, sectioned at 5 µm thickness and stained with haematoxylin and eosin (H & E).

Histologically, ovaries from the full-term guanaco revealed a number of tertiary Graafian follicles with a fluid-filled antrum, and many primordial and secondary follicles throughout the outer cortex, with oocytes surrounded by single or multiple layers of follicle cells (figure 3*a*). The ovaries of the camel foetus contained numerous large tertiary follicles, of up to 0.5 cm in diameter, and many primordial and secondary follicles throughout the outer ovarian cortex.

The ovaries of the three hybrids presented a very different appearance. GC1, stillborn at 365 days, showed heavily eosinophilic oogonia arranged in clumps or cords, but there was no evidence that any of the oogonia had entered meiosis as there were no signs of any oocytes with their characteristic layer of surrounding follicle cells (figure 3*c*). CG2, also stillborn at 365 days, showed a compact, fibrous ovarian cortex with many eosinophilic cords which may represent dead or dying oogonia that were unable to enter meiosis (figure 3*b*). There were occasional degenerating oocytes with surrounding follicle cells. The ovaries of CG1, aborted at 291 days, showed a similar picture, with an occasional degenerate-looking oocyte surrounded by degenerating follicle cells, suggesting that a few oogonia had been able to initiate meiosis. However, chromosomal pairing was probably incomplete and resulted in the death of the oocyte and follicle cells that it had induced to form around itself (figure 3*d*).

(c) *Parentage analysis*

Blood samples were collected into preservative-free sodium heparin tubes from the two male camels, Musehan and Young One, that had supplied the semen used for artificial insemination; from guanaco no. 1, the mother of the calf; and from Rama the calf (CG5, see table 1). DNA was extracted from a 5 ml aliquot of whole blood using a commercial kit (Nucleon; Scotlab Ltd, Coatbridge, Scotland). Subsequently, genotypes for each animal were obtained by performing PCR on the extracted DNA, using eight llama microsatellites under the PCR conditions described by Lang *et al.* (1996). Fluorescent dUTP was incorporated into the PCR products which were then electrophoresed on an ABI377 automated sequencer and the data analysed using Genescan 2.1.

The results of the genotyping analysis using the llama microsatellites are presented in table 2. They are fully consistent with the hybrid being the offspring of the female guanaco and the male camel, Musehan, with exclusion of the second male camel, Young One, on the basis of two of the markers, YWLL08 and YWLL44. The size ranges for the alleles amplified from the guanaco sample were all within the ranges published by Lang *et al.* (1996), except those of markers YWLL19 and YWLL44. The variation observed with YWLL44 was relatively small, the observed alleles being 83/112, compared with the published range of 86–120. However, for YWLL19, the size of the observed allele (243) differed significantly from the published size range of 137–161.

4. DISCUSSION

To our knowledge, this is the first report of a viable hybrid between Old and New World camelids. It was achieved by using artificial insemination and hormone therapy to overcome the marked differences between the two parental species in terms of their body size and their oestrous behaviour (England *et al.* 1971; Skidmore *et al.* 1996*b*). Considering the other marked anatomical, physiological and behavioural differences that have evolved between the two separated groups to enable them to survive in very harsh and diametrically opposed enviroments, it is quite remarkable that their basic reproductive mechanisms have been sufficiently conserved to permit hybridization. Although the diploid chromosome number has remained unchanged at $2n = 74$ for all camelids, the failure of meiosis in the ovaries of all the hybrids suggests that sufficient genetic change must have

occurred during the millions of years of reproductive isolation to disrupt the pairing of homologous chromosomes as they enter meiosis. It remains to be seen whether the surviving male hybrid will be capable of producing any sperm when he reaches puberty, although this seems most unlikely.

The conception rates achieved when inseminating dromedaries with semen from a single male guanaco (two conceptions from the insemination of 30 fertile females on 50 separate occasions) and guanacos with semen from two dromedary males of known fertility (six conceptions from the insemination of nine animals on 34 occasions) were much lower than the 50–55% conception rate achieved routinely in the same laboratory when inseminating dromedaries with dromedary semen. This might indicate impaired fertilization and/or early embryonic development. The conception rate appeared to be higher in guanacos inseminated with dromedary semen than in the dromedaries inseminated with guanaco semen, which is reminiscent of the difference in fertility between other reciprocal interspecific mammalian matings, such as between rabbit and hare (Chang *et al*. 1964), sheep and goat (Hancock *et al*. 1968), and horse and donkey (Allen & Short 1997). It could be explained by differences in sperm–egg binding; camel spermatozoa might bind more readily to guanaco oocytes than vice versa. The causes of the late foetal deaths and stillbirths in the camelid hybrids remain unexplained.

DNA genotyping was used to confirm that the hybrid was the product of the mating between the female guanaco and a male dromedary camel and it also determined the actual sire between the two possible contenders. The combined exclusion probabilities of the eight microsatellites used, based on their individual exclusion probabilities in llamas and alpacas, is 0.9997. While the corresponding exclusion probability in Old World camelids has not been determined, it would be surprising if this panel of microsatellites did not display useful polymorphism in both the Bactrian and dromedary camels. The allele size observed with the marker YWLL19 in all four animals typed here (243 bp) differs significantly from the published allele size range in llamas and alpacas (137–161 bp). The primer sequences for YWLL19 were verified as correct and no obvious explanation exists for this discrepancy. It was of interest to find that the allele sizes observed with the camel samples for five of the markers (YWLL08, YWLL19, YWLL29, YWLL36 and YWLL40) fell outside the ranges for these markers observed in llamas and alpacas, thereby suggesting that these microsatellites have diverged considerably in Old and New World camelids since their split 11–30 Myr ago.

Perhaps one of the most interesting aspects of this study relates to the gestation length and size at birth of the surviving hybrid. The duration of gestation (328 days) and birth weight (5.5 kg) are close to the normal range for guanaco pregnancy, but are significantly less than the $\pm$395 days $\pm$30 kg of a normal dromedary pregnancy. Thus, there appears to have been a complete maternal override of the paternal genotype during pregnancy, which is perhaps a result of the size constraint imposed by a restricted area of the endometrium upon the diffuse, non-invasive epitheliochorial placenta. Once born, however, the hybrid calf had shown significant catch-up growth and at nine months of age was 2.5 cm taller than his mother. It will be interesting to see whether this pronounced intra-uterine growth retardation has any adverse effects on his subsequent health and well-being, as the Barker hypothesis (Barker 1995) would predict.

The apparent female skewing of the sex ratio in the foetuses and neonate (one male:five females) is in accordance with Haldane's law, which states that 'when in the F_1 offspring of two different animal species one sex is absent, rare or sterile, that sex is the heterozygous sex' (Haldane 1922). The reason for this skewing may be that the mutation rate of genes of the unpaired segment of the Y chromosome is apparently much higher than that of genes on any other chromosome (Short 1997*a*). This is because any genetic defects cannot be 'repaired' by meiotic crossing over with a homologous chromosome. Furthermore, the Y chromosome never enters female germ cells, and germ-line mutations are known to be far more common in the testis than the ovary (Short 1997*a*,*b*). Considering the many millions of years of reproductive isolation of the dromedary and the guanaco, it is perhaps surprising that any male hybrids were produced at all. Rama is living proof that the sex-determining genes on the camel Y chromosome are still capable of inducing testicular development in the hybrid. However, it seems likely that Rama will prove to be sterile, both because of the generalized meiotic failure observed in the ovaries of the hybrids, and the expected differences between Y-linked spermatogenesis-determining genes in the dromedary and the guanaco.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.